Reference: *Biol. Bull.*, 136: 9–27. (February, 1969)

THE TUBIFICIDAE (ANNELIDA, OLIGOCHAETA) OF CAPE COD BAY WITH A TAXONOMIC REVISION OF THE GENERA *PHALLODRILUS* PIERANTONI, 1902, *LIMNODRILOIDES* PIERANTONI, 1903 AND *SPIRIDION* KNOLLNER, 1935 [1]

DAVID G. COOK

Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

The marine Tubificidae are an abundant, widely distributed, but poorly known group of Oligochaeta. The most recent account dealing with the fauna of the Cape Cod area is that of Moore (1905) who recognized seven species, mainly from littoral and estuarine environments. Material from a survey of the fauna of Cape Cod Bay which is being conducted by the Biotic Census of the Systematics-Ecology Program was found to contain a number of species which Moore did not see, five of these being new to science.

Two of the species described here, *Phallodrilus obscurus* nov. sp., and *Peloscolex intermedius* nov. sp., are very closely related to some species described by earlier workers and differ from them only in minor details. However, two considerations are thought to be sufficient justification for describing them as new species. Firstly, the available descriptions of closely related species are generally poor and cannot be augmented at present as type material is not available. Secondly, even when descriptions are adequate and type series are available for comparison, material tends to be from widely separated geographical areas, and without more extensive collections it is impossible to decide whether the differences observed are due to a wide intraspecific variation over the species range, discontinuous variation meriting subspecific rank, or real specific differences. In this situation, where the taxa are morphospecies in the sense of Cain (1954), it is proposed that the least confusing action from the nomenclatural point of view, where doubt exists, is to keep specific limits narrow, erect new species names and synonomize, if necessary, when type material becomes available for the old species.

At the generic level some rearrangments have been necessary to clarify definitions and to attain consistency between them. The major characters on which this has been based are the nature and position of the prostate glands and the form of the atria. Thus in *Clitellio* Savigny, 1820 (Fig. 1a) the prostate gland is lacking, or is a diffuse layer covering the long cylindrical atrium, while in *Limnodriloides* Pierantoni, 1903 (Fig. 1b) the prostate is a discrete organ with the attachment to the relatively short atrium localized to a small area. In *Spiridion* Knollner, 1935 (Fig. 1c) the attachment is further localized so that the prostate is truly penduncu-late and joins the atrium apically rather than subapically to medially as in *Limnodriloides*. *Aktedrilus* Knollner, 1935 is synonomized with *Phallodrilus* Pierantoni, 1902 (Fig. 1d) on the basis of their common possession of two thickly-stalked prostate glands, attached to each short cylindrical atrium.

[1] Contribution No. 162 from the Systematics-Ecology Program.

Methods

The Biotic Census of Cape Cod Bay is a continuing long term investigation of the fauna of this area. Samples are taken uniformly over the area of the Bay at predetermined locations on a grid of nautical mile squares. Quantitative samples are being taken with a Smith-McIntyre grab in the middle and at each corner of every alternate quadrat. Material is being washed through a series of screens down to 0.5 mm mesh diameter, narcotized in propylene phenoxytol, fixed in formalin and stored in 80% ethyl alcohol. Oligochaeta from 27 completed samples (1.0 mm screen fraction) and two unsorted samples (0.5 mm screen fraction) were examined.

The anatomy of the Tubificidae was studied microscopically by one, or a combination of, three methods: a) worms were lightly stained in acetic haematoxylin and mounted whole in Canada Balsam, b) the genitalia were dissected out of stained worms using sharpened needles and forceps, and the parts mounted in

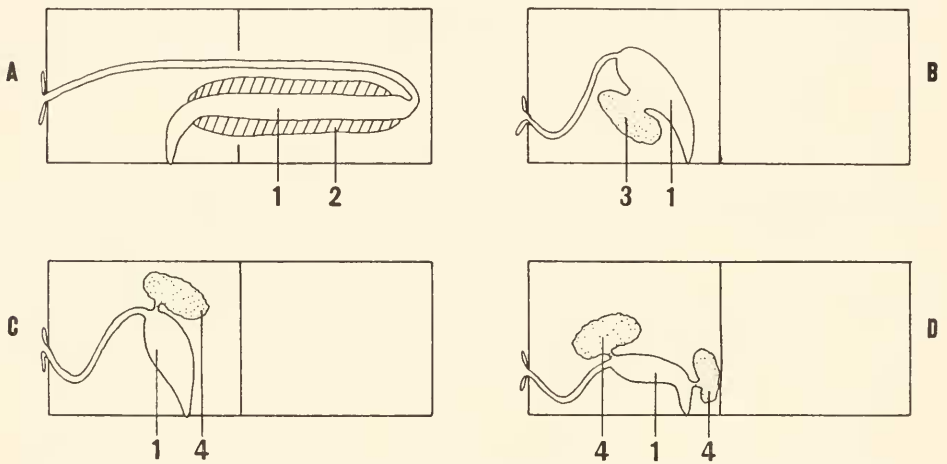

Figure 1. Diagrammatical representation of the male genitalia of A. *Clitellio;* B. *Limnodriloides;* C. *Spiridion;* D. *Phallodrilus.* 1. Atrium; 2. Diffuse prostate, absent in *C. arenarius;* 3. Discrete prostate, thickly-stalked; 4. Discrete prostate, pedunculate.

Canada Balsam, c) the genital regions of the worms were sectioned at 7 μ and stained in haematoxylin and eosin.

Species Examined from Cape Cod Bay

(?) *Tubifex longipenis* Brinkhurst, 1965. Southwest sector,[2], 7 to 18 meters depth. The three individuals attributed to this species from the Cape Cod Bay material were of similar size and setal pattern to the type specimens. However, they were immature and thus their identity must remain uncertain until mature material is available.

[2] In this list "sector" refers to an approximate distribution of species on the following basis: Cape Cod Bay is considered as roughly circular in area; the four sectors correspond to the areas enclosed by bisecting this circle from north to south, and from east to west at 41°54′ N, 70°17′ W.

Peloscolex benedeni (Udekem, 1855). Southwestern sector, 7 to 18 meters depth. This species seems to be confined to shallow waters and is locally very abundant.

Peloscolex intermedius nov. sp. The two Northern, and Southwestern sectors, 7 to 46 meters depth.

Adelodrilus anisosetosus nov. gen., nov. sp. Southeastern sector, 18 meters depth.

Phallodrilus obscurus nov. sp. Southwestern sector, 8.5 meters depth.

Phallodrilus coeloprostatus nov. sp. Southeastern sector, 18 meters depth.

Limnodriloides medioporus nov. sp. The two Southern, and Northeastern sectors, 7 to 46 meters depth. This entity, and *P. intermedius,* are the dominant Tubificidae in Cape Cod Bay below 30 meters depth.

Systematic Section

Peloscolex intermedius nov. sp.

Figure 2

Holotype. United States National Museum (USNM) Cat. No. 38259. Cape Cod Bay, Massachusetts, USA. 41°55.75′ N, 70°21.07′ W. Depth 42.6 meters.

Paratypes. USNM 38260. Six individuals as type locality; 38261 one individual from 42°0.5′ N, 70°24′ W. Depth 36.5 meters; 38262 one individual from 41°55.4′ N, 70°15.9′ W, depth 42.6 meters.

Derivation. "Intermediate" between two other *Peloscolex* species.

Description. Length 8 to 10 mm, diameter 0.28 to 0.45 mm. About 42 segments. Prostomium small, conical, with small papilla anteriorly. Body wall smooth to densely, but very finely, granulate. Dorsal setae; from segment II to VI (sometimes VII) 3 bifids and 1 to 3 hairs per bundle present; bifids 50 to 80 μ long with equal teeth which become increasingly shorter in more posterior segments, or whose upper tooth becomes increasingly reduced; hairs 110 to 160 μ long, bearing a few very short, indistinct, lateral hairs; from segment VII (sometimes VIII) to the terminal segment, 3 simple-pointed, hair-like setae, 75 to 100 μ long plus 3 true hair setae, 110 to 160 μ long per bundle present. Ventral setae; anteriorly 3 to 4 per bundle, posteriorly 2 to 3 per bundle; ventral bifids, 60 to 80 μ long, with thin upper tooth and broad widely diverging lower tooth (Fig. 2b). One unmodified ventral seta per bundle on segments X and XI. One pair male and spermathecal pores situated just anterior to, and in line with ventral setae.

Looped to coiled vasa deferentia, 15 μ diameter, 1.0 mm long, join atria subapically and dorsally. Vasa deferentia 5 to 7 times longer than atria. Atria elongate, with long axis directed posteriorly and with muscle bands arranged circularly. Atria 150 to 220 μ long, 60 to 90 μ wide, joined to cylindrical, cuticularized penes, 75 to 100 μ long, 31 to 37 μ wide, by short, discrete proximal ducts. Large, discrete prostate glands join atria subapically to medially and ventrally (Fig. 2a). Spermathecae with sacciform ampullae and long discrete ducts which have a bulbous swelling proximally. Spermatophores spindle-shaped, 130 μ long, 35 μ diameter at the median swelling.

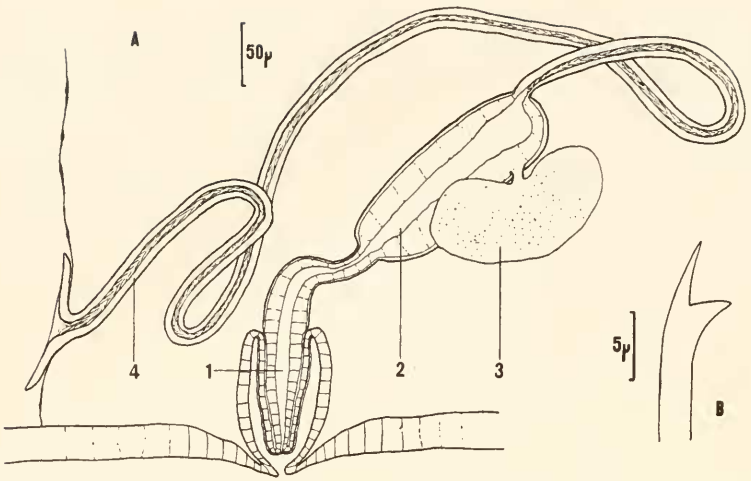

FIGURE 2. *Peloscolex intermedius* nov. sp. A. Male genitalia; B. Posterior ventral seta. 1. Cuticularized penis; 2. Atrium; 3. Prostate; 4. Vas deferens.

DISTRIBUTION. Known only from Cape Cod Bay, Massachusetts, in waters 7 to 46 meters deep.

REMARKS. *P. intermedius* is closely related to *P. apectinatus* Brinkhurst, 1965 and *P. swirencowi* (Jaroschenko, 1948). (Table 1.) These three species, together with *P. euxinicus* Hrabě, 1966, *P. gabriellae* Marcus, 1950 and *P. nerthoides* Brinkhurst, 1965, form a complex of small, sparsely or finely papillate, marine worms whose male genitalia bear a strong resemblance to those of *Tubifex*. It is suspected that future work on this group of species may reveal more intermediate forms in the complex which will invalidate many of the entities or reduce them to subspecific rank, and that such work will make necessary a critical reexamination of the generic limits of *Peloscolex* and *Tubifex*.

TABLE I

Differences between Peloscolex intermedius *nov. sp. and its two most closely related species,* P. apectinatus *and* P. swirencowi

Character	*P. intermedius*	*P. apectinatus*	*P. swirencowi*
Hair setae	With sparse lateral hairs	Serrate	Smooth
Anterior dorsal setae	Bifid to seg. VI	Bifid	Bifid to seg. VIII
Posterior dorsal setae	Single-pointed, elongate	Bifid	Single-pointed, elongate
Ventral setae; upper tooth compared to lower	Longer	Same or shorter	Longer
Length vas deferens/ length atrium	4.5	less than 3	2.5
Length penis/diameter penis	2.4–2.6	1.5–1.6	1.0

Adelodrilus nov. gen.

Derivation. "Adelo-" = Gr. hidden/secret; "drilus" = worm.

Definition. Hair setae absent. Penial setae highly modified. Male and spermathecal pores paired in line of ventral setae.

Vasa deferentia very short, about 0.2 the length of the atria, join the latter apically. Atria thin walled, cylindrical, without connection with prostate cells, terminating in pear-shaped penial bulbs. Penial bulbs each bear two large, thickly-stalked, prostate glands. Spermatophores not developed. Coelomocytes small and only sparsely distributed.

Type-species. *Adelodrilus anisosetosus* nov. sp. by monotypy.

Adelodrilus anisosetosus nov. sp.

Figure 3

Holotype. USNM 38251. Cape Cod Bay, Massachusetts, USA. 41°53.5′ N, 70°10.65′ W. Depth 18.3 meters.

Paratypes. USNM 38252. Six individuals; locality as for Holotype.

Derivation. "Aniso-" = Gr. unequal; "setosus" = setae.

Description. Length 4 to 6.5 mm, diameter 0.18 to 0.4 mm. 30 to 45 segments. Prostomium broadly rounded, longer than it is wide at peristomium. Clitellum well developed on segments X to XII. Segments, especially in posterior part of body, deeply annulated with body wall nuclei concentrated in rows on the crests of the ridges formed by annuli. Annuli impart granular to papillate appearance to body wall. Setae 3 sometimes 4, per bundle in all body regions. Anterior, and posterior ventral, setae are bifid with widely diverging teeth, the upper of which become thinner and shorter in more posterior segments (Fig. 3b, c). Posterior dorsal setae single-pointed and strongly curved distally, 85 to 110 μ long (Fig. 3d). Anterior setae 80 to 100 μ long and mid body setae 70 to 75 μ long. Ventral setae of segment XI highly modified into penial bundles, each of which contains one giant, simple-pointed, strongly curved seta, 135 to 150 μ long, 6.5 to 8.8 μ thick, and 8 to 12 small, thin, straight setae, 70 to 90 μ long, 1.5 μ thick, which are clubbed distally and which bear a thin, hooked tooth, originating apically and curving around the club (Fig. 3e, f). Male and spermathecal pores paired in line of ventral setae.

Pharyngeal glands extend into segment VI. Male ducts consist of a pair of vasa deferentia, 40 μ long, 15 μ diameter, which join a pair of cylindrical, thin-walled atrial ampullae apically. Each atrial ampulla, 250 μ long, 28 to 37 μ diameter, joins a pear-shaped penial bulb. This structure, 50 to 65 μ long, 30 to 45 μ diameter, bears two thickly-stalked, discrete prostate glands, one apically near atrial junction, and one near the proximal end. Penial bulbs open into a pair of spherical pedunculate chambers about 70 μ diameter, into which also protrude the penial setae

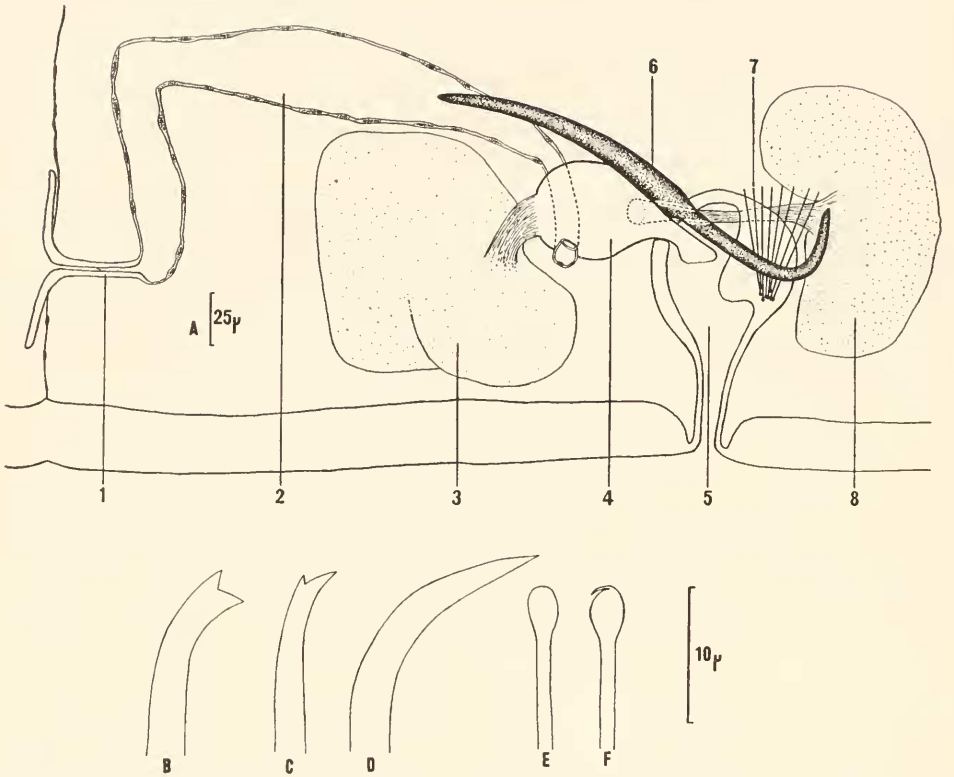

FIGURE 3. *Adelodrilus anisosetosus* nov. gen., nov. sp. A. Male genitalia; B. Anterior seta; C. Posterior ventral seta; D. Posterior dorsal seta; E, F. Small straight penial setae showing two aspects of distal club. 1. Vas deferens; 2. Atrium; 3. Anterior prostate; 4. Penial bulb; 5. Penial chamber; 6. Giant penial seta; 7. Small straight penial seta; 8. Posterior prostate.

(Fig. 3a). Penes are formed from the protruded ends of elongate lining cells of the penial bulb. Spermathecae with sacciform ampullae 200 μ long, up to 55 μ wide, and ill-defined ducts, 45 μ long, 25 μ diameter which open near septum IX/X.

DISTRIBUTION. Known only from type-locality.

REMARKS. The homologies of the male ducts of *Adelodrilus anisosetosus* are difficult to interpret. Thus the penial bulb (Fig. 3) is probably not equivalent morphologically to this structure in other Tubificidae. Morphogenetic studies are clearly necessary on this and on some related genera (see below) to clarify these anatomical details. From the functional point of view, however, this entity is unique among the tubificids in possessing prostate glands which are associated with a penial structure and in having two distinct modifications of the penial setae. The structure of the penis itself is also interesting in that it is formed from the internal lining cells of the penial bulb which are thought to become elongate at copulation. Such a

penial structure has only been reported in the Lumbriculidae (Cook, 1967) and the Dorydrilidae (Cook, 1967; 1968).

It is possible that *Adelodrilus* is phylogenetically important as it may elucidate the nature and origin of the bulbous "paratria" found in *Bothrioneurum* Stolc, 1888 and *Smithsonidrilus* Brinkhurst, 1966 (Fig. 4). In both of these genera a cylindrical atrium and a bulbous "paratrium" enter a common chamber. It seems possible that in *Smithsonidrilus* the secretory and the storage functions of the male genital apparatus have become morphologically separated and that *Adelodrilus* is close to the ancestral form from which it and *Bothrioneurum* diverged. As a corollary to this hypothesis, the intromittent function of the penis must have become relocated in the storage part of the atria, or that this function became redundant by virtue of the presence of an eversible chamber acting as a pseudopenis in the sense of Brinkhurst (1965a).

Phallodrilus Pierantoni, 1902

DEFINITION. Hair setae absent. Ventral setae of segment XI usually modified. Male pores paired, near ventral setae. Spermathecal pores paired, lateral to near ventral setae, or unpaired, mid dorsal.

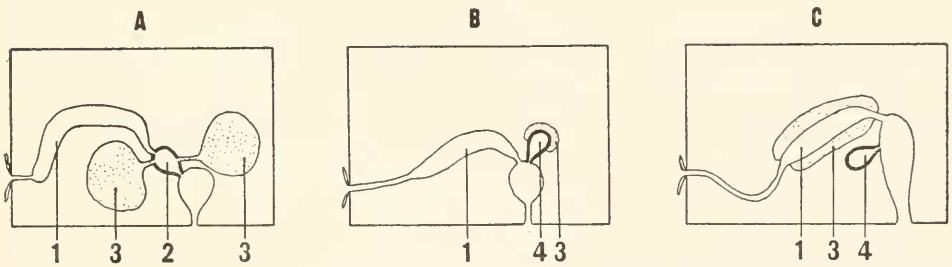

FIGURE 4. Diagrammatic representation of the male genitalia of A. *Adelodrilus;* B. *Smithsonidrilus;* C. *Bothrioneurum.* 1. Atrium; 2. Penial bulb; 3. Prostate; 4. "Paratrium."

Vasa deferentia as long as, or slightly longer than pear-shaped to cylindrical atria. Vasa deferentia join atria apically. Each atrium bears two discrete, pedunculate prostate glands, one of which joins near the vas deferens, the other near the proximal end of the atrium. Spermatophores not developed. Coelomocytes sparse to absent.

TYPE SPECIES: *Phallodrilus parthenopaeus* Pierantoni, 1902.

REMARKS. As defined above, *Phallodrilus* includes *Aktedrilus* Knollner, 1935. The only character which has been used to keep these two genera separate in the past has been that *Aktedrilus* possesses only a single, dorsal spermatheca. However, this separation is considered to be invalid due to the fact that in *Phallodrilus coeloprostatus* the spermathecal pores are more dorsal than ventral, and that in some other genera paired versus unpaired spermathecae are clearly specific characters (*e.g., Monopylephorus, Eclipidrilus* (Lumbriculidae)).

KEY TO SPECIES.

1. Penial setae absent. Spermatheca unpaired, with mid-dorsal pore.....*P. monospermathecus* (Knollner, 1935)
Penial setae present. Spermathecae paired, with lateral to ventral pores....2
2(1). Up to 13 hooked penial setae, shorter than body setae, present. Spermathecal pores situated between lines of dorsal and ventral setae.....*P. coeloprostatus* nov. sp.
Up to 7 bifid to simple-pointed penial setae, longer than body setae, present. Spermathecal pores situated near to ventral setae.....3
3(2). Spermathecal setae with upper teeth 2.5 times longer than lower teeth.....*P. parthenopaeus* Pierantoni, 1902.
No modified spermathecal setae.....4
4(3). 4 to 6 (rarely 7) unmodified to single-pointed penial setae present. Spermathecal ducts short and narrow.....*P. aquaedulcis* Hrabě, 1960
2 to 3 (rarely 4) single-pointed penial setae present. Spermathecal ducts long and thick.....*P. obscurus* nov. sp.

Phallodrilus coeloprostatus nov. sp.

Figure 5

HOLOTYPE. USNM 38257. Cape Cod Bay, Massachusetts, USA. 41°53.5′ N, 70°10.65′ W. Depth 18.3 meters.

PARATYPES. USNM 38258. Six individuals; locality as for Holotype.

DERIVATION. "Coelo-" = Gr. hollow; "prostatus" = prostate.

DESCRIPTION. Length 6 to 10 mm, diameter 0.17 to 0.30 mm. 58 to 60 segments. Prostomium rounded, as long as, or a little longer than it is broad at peristomium. Clitellum well developed on segments 1/2X to XII. Setae bifid with upper teeth shorter and thinner than lower, 48 to 55 μ long; 4 to 5 per bundle anteriorly, 3 to 4 posteriorly (Fig. 5c). Ventral setae of segment X unmodified. 10 to 13 penial setae, 40 to 45 μ long, hooked distally, present on segment XI (Fig. 5d). Paired male pores situated just lateral to penial setae. Paired spermathecal pores situated in anterior part of segment X, mid way between lines of dorsal and ventral setae.

Pharyngeal glands extend into segment VI. Chlorogogen cells begin in segment VI. Atria very small, cylindrical, curved towards anterior end of animal and very closely applied to body wall (Fig. 5a). Vasa deferentia, 6 μ diameter, longer than atria, join latter apically. Atria 95 to 130 μ long, 19 to 26 μ diameter, with very thin musculature and thick lining cells, terminating in small, truncated cone-shaped penes. Two pairs of very large prostate glands join atria by thick, discrete ducts, one near vasa deferentia, the other posteriorly, near the proximal end of the atria. Prostates, which lie medially to, and completely cover atria, have distinct boundaries, but the cells are loosely packed and cavities form between them (Fig. 5b). Paired spermathecae have short, discrete ducts and large ovoid to elongate ampullae.

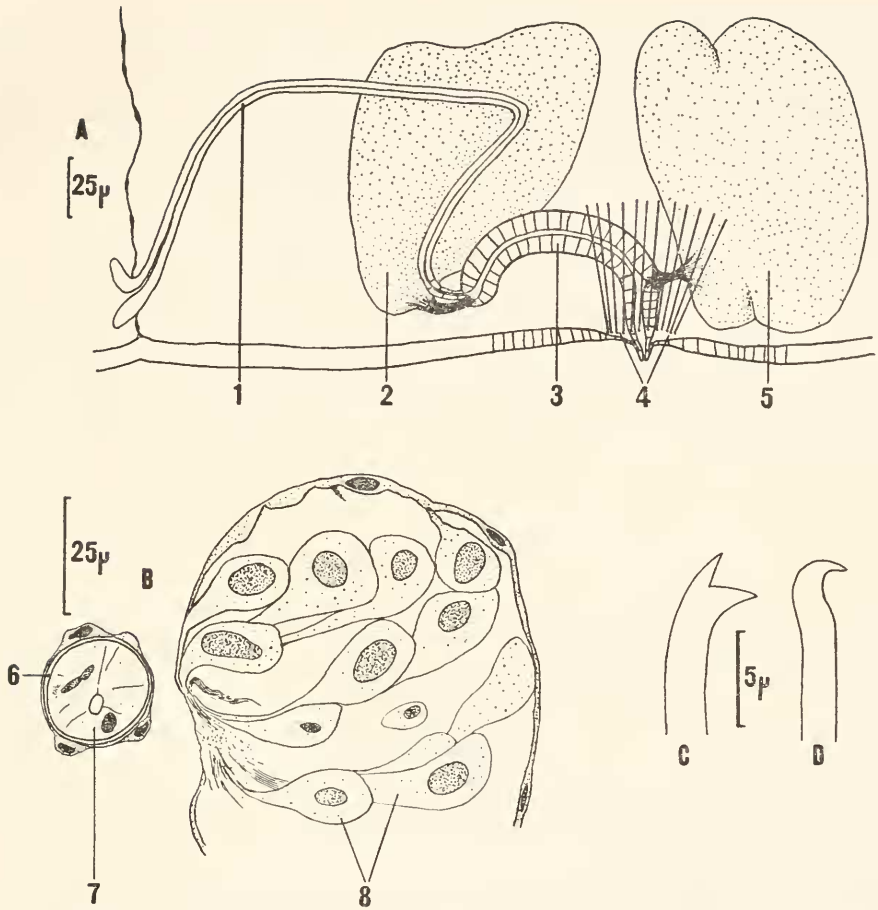

FIGURE 5. *Phallodrilus coeloprostatus* nov. sp. A. Male genitalia; B. Transverse section of atrium and prostate gland; C. Seta; D. Penial seta. 1. Vas deferens; 2. Anterior prostate; 3. Atrium; 4. Penial setae; 5. Posterior prostate; 6. Atrial wall; 7. Atrial lining cells; 8. Prostate cells.

DISTRIBUTION. Known only from type-locality.

Phallodrilus obscurus nov. sp.

Figure 6

HOLOTYPE. USNM 38255. Cape Cod Bay, Massachusetts, USA. 41°51.0′ N, 70°31.1′ W. Depth 8.5 meters.

PARATYPES. USNM 38256. Six individuals; locality as for Holotype.

DERIVATION. "Obscure" relationship to other species of the genus.

Description. Length 7 mm, diameter 0.16 to 0.20 mm. 40 segments. Prostomium longer than it is broad at peristomium. Setae, except ventrals of segment XI, bifid with upper tooth equal to, or shorter and thinner than lower tooth (Fig. 6b). Setae 45 to 55 μ long, 4 to 6 per bundle anteriorly, 4 to 5 per bundle posteriorly. Ventral setae of segment X unmodified. 2 to 3 (rarely 4) slightly curved, simple-pointed penial setae, 55 to 70 μ long, present (Fig. 6c). One pair spermathecal pores in anterior part of segment X, in line with ventral setae. Male pores just lateral to penial setae.

Pharyngeal glands extend into segment V. Chlorogogen cells begin in segment VI. Atria pear-to-comma-shaped, shorter than vasa deferentia which join atria apically. Vasa deferentia 100 to 130 μ long, 5.5 to 7.5 μ diameter. Atria 70 to 120 μ long, 30 to 35 μ diameter. Anterior prostate gland enters atrium near vas deferens, posterior one 10 to 40 μ from the male pore (Fig. 6a). Penes absent. One pair spermathecae with long, thick ducts and cylindrical ampullae, open near septum IX/X.

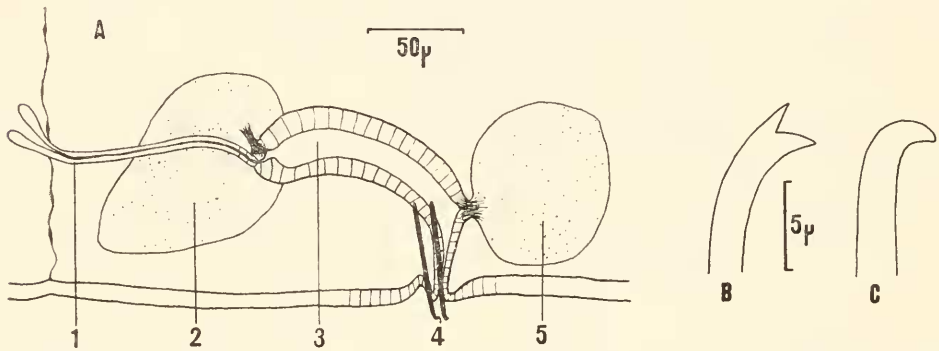

Figure 6. *Phallodrilus obscurus* nov. sp. A. Male genitalia; B. Seta; C. Penial seta. Explanations as in Figure 5.

Distribution. Known only from type-locality.

Remarks. *P. obscurus* is very closely related to *P. parthenopaeus* and *P. aquaedulcis*. These three entities form a complex whose taxonomic rank is uncertain. It is possible that they are subspecies or merely intra-specific variants or differing stages of maturation.

Phallodrilus parthenopaeus Pierantoni, 1902

Phallodrilus parthenopaeus Pierantoni, 1903, pp. 114, 115, fig. 1, 2: Hrabě, 1960, p. 251: Brinkhurst, 1963a, p. 74; 1963b, p. 714; 1967, p. 115.

Type-material. Not designated and not located. Type-locality Gulf of Naples, Italy. Depth 4 meters.

Description, (from literature). Length up to 12 mm, diameter 0.2 mm. 40 to 60 segments. Setae, except ventral of segments X and XI, bifid with equal teeth. 4 setae per bundle anteriorly, 2 per bundle posteriorly. 2 spermathecal setae per bundle with upper teeth about 2.5 times longer than lower. 2 straight, blade-shaped penial setae per bundle, with simple, rounded ends. Male and spermathecal pores paired, near line of ventral setae.

Atria elongate pear-shaped, shorter than vasa deferentia which join atria apically. Anterior prostate gland opens near vas deferens, posterior one near base of atrium. Penes absent. Spermathecae paired in segment X.

Distribution. Known only from type-locality.

Phallodrilus aquaedulcis Hrabě, 1960

Phallodrilus aquaedulcis Hrabě, 1960, pp. 248–251, fig. 1–4: Brinkhurst, 1963a, pp. 74, 77.

Type-material. Hrabě collection; catalogue numbers not designated. Locality, Blumenthal, River Weser, Germany. In fresh-water.

Description, (from literature). Length 3 to 4 mm, diameter 0.15 mm. 28 to 32 segments. Prostomium rounded, as long as it is broad at peristomium. Setae, except ventrals of segment XI, bifid with upper tooth thinner and shorter than lower, about 42 μ long. 3 to 4 (rarely 5) setae per bundle anteriorly, 2 per bundle posteriorly. Ventral setae of segment X unmodified. 4 to 6 (rarely 7) penial setae present; these unmodified bifids to single-pointed setae. Spermathecal pores in anterior part of segment X, in line with ventral setae. Male pores slightly anterio-lateral to penial setae.

Pharyngeal glands present in segments III to V. Chlorogogen cells begin in segment V or VI. Atria cylindrical, longer than vasa deferentia which open into atria apically. Anterior prostate gland opens near vas deferens, posterior one near proximal part of atrium. Penes absent. Spermathecae paired, with long, cylindrical ampullae and short, narrow ducts.

Distribution. Known only from type-locality.

Phallodrilus monospermathecus (Knollner, 1935) nov. comb.

Aktedrilus monospermathecus Knollner, 1935, pp. 482–491, fig. 43–50: Bulow, 1955, p. 262; 1957, p. 102: Hrabě, 1960, pp. 251–254, fig. 5–12: Cekanovskaya, 1962, p. 286: Brinkhurst, 1963a, p. 75; 1963b, p. 714; 1963c, p. 1203; 1964, p. 12; 1967, p. 115.

Type-material. Not designated and not located. Type-locality, Kiel Bay, West Germany, Marine, littoral.

Other material. R. O. Brinkhurst collection; many individuals from saline moat, Hale, Lancashire, England.

Description, (from literature, some characters confirmed by author). Length 3 to 8 mm, diameter 0.11 to 0.23 mm. 25 to 35 segments. Prostomium longer than it is broad at peristomium. Setae bifid with upper tooth shorter and thinner than lower, 32 to 45 μ long. 3 to 4 (rarely 2 to 5) setae per bundle anteriorly, 2 to 3 (rarely 1 to 4) per bundle posteriorly. Ventral setae of segment XI absent. Spermathecal pore single, mid-dorsal on segment X; cuticle thickened in region of pore. Male pores paired in line of ventral setae.

Pharyngeal glands in segments IV to VI. Chlorogogen cells begin in segment VI. Atria narrow, cylindrical, about as long as vasa deferentia. Atria, 16 to 17 μ diameter, terminate in ovoid penes 25 to 30 μ long, 17 to 19 μ wide, contained in penial chambers. Anterior prostate glands open into atria apically with vasa deferentia, smaller posterior prostates enter near proximal end of atria. Spermatheca single, cylindrical, with thick duct opening mid-dorsally.

Distribution. Mainly intertidal zone of the Baltic Sea, Mediterranean Sea and Northeastern Atlantic. Also brackish-water and ground-water.

Limnodriloides Pierantoni, 1903

Definition. Hair setae absent. Ventral setae of segment XI unmodified. Male and spermathecal pores paired, more or less in line with ventral setae, or contained within a large, common, mid-ventral fold.

Gut in immediate preclitellar region with a pair of elongate diverticulae. Vasa deferentia, as long as or slightly longer than atria, join latter more or less apically. Each atrium bears a discrete prostate gland, broadly attached ventral or anterior to vas deferens. Atria with thin muscle layer. Penes present or absent. Spermatophores absent but sperm often aggregates into more or less discrete, oriented bundles. Coelomocytes absent.

Type-species. *Limnodriloides appendiculatus* Pierantoni, 1903.

Remarks. *Limnodriloides* was included in *Clitellio* by Brinkhurst (1963a) but was reinstated by Hrabě (1967) who included *Thallassodrilus prostatus* (Knollner, 1935) within it. *Limnodriloides* is considered to be distinct from *Clitellio* by virtue of three contrasting criteria, thus: *Limnodriloides* has 1) gut diverticulae, 2) broadly attached, discrete prostate glands, and 3) no spermatophores while *Clitellio* possesses 1) no gut diverticulae, 2) no prostate gland or a diffuse one, and 3) well developed spermatophores (see also Fig. 1). *T. prostatus* (Knollner) is excluded from *Limnodriloides* as it has no gut diverticulae, possesses a series of penial setae, and has a peculiarly thick muscular atrium with a pedunculate prostate gland.

In his original description of the genus, Pierantoni (1904) included the species *L. roseus* and *L. pectinatus* in *Limnodriloides*. These two species have no gut diverticulae, the former have pedunculate prostate glands joining the atria dorsal or posterior to the vasa deferentia, and the latter possesses a series of modified penial setae. Neither species has apparently been seen by other workers who have regarded them as *species dubiae* of *Limnodriloides*. Since *Spiridion* Knollner, 1935, has penial setae and pedunculate prostate glands which join the atria dorsal or posterior to the vasa deferentia, it is proposed that *L. roseus* and *L. pectinatus*

should be included as *species dubiae* of this genus. This action clarifies the definitions of this group of marine genera as *Limnodriloides,* excluding *L. roseus* and *L. pectinatus,* becomes a clearly homogeneous group, while *Spiridion,* even with its new *species dubiae,* retains its cohesion as a genus.

Key to species.

1. Male and spermathecal pores contained within a median ventral fold in body wall; *i.e.,* external apertures appear as elongate median slits arranged transversely.....*L. medioporus* nov. sp.
   Male and spermathecal pores paired, in line of ventral setae; *i.e.,* external apertures appear as simple, paired pores.....2
2(1). Ventral setae of segment X modified and contained within a muscular sac.....*L. winckelmanni* Michaelsen, 1914
   Ventral setae of segment X unmodified or absent.....3
3(2). Gut diverticulae in segment VIII. 2 setae per bundle in most posterior segments.....*L. appendiculatus* Pierantoni, 1903
   Gut diverticulae in segment IX. 1 seta per bundle in most posterior segments.....*L. agnes* Hrabě, 1966

Limnodriloides medioporus nov. sp.

Figure 7

Holotype. USNM 38253. Cape Cod Bay, Massachusetts, USA. 41°54.9′ N, 70°15.2′ W. Depth 36.5 meters.

Paratypes. USNM 38254. Seven individuals; locality as for Holotype.

Other material. Author's collection, from Woods Hole Oceanographic Institution's Gay Head—Bermuda transect: 40°20.5′ N, 70°47′ W, depth 97 meters (8 individuals).

Derivation. "Medio-" = L. middle; "porus" = pore/hole.

Description. Length 8 mm, diameter 0.2 mm. 40 segments. Prostomium usually longer than it is broad at peristomium, with a small, thin-walled papilla on its tip. Setae 2 to 4 per bundle anteriorly, 2 per bundle posteriorly. Setae bifid with teeth of about equal length, 30 to 50 μ long (Fig. 7c). Ventral setae absent on segments X and XI. Clitellum on segments IX to XII. One pair of spermathecal pores open ventral to line of ventral setae and are joined by a laterally elongated, median invagination of the body wall of segment X. One pair male pores open inside a dumbell-shaped, median bursa on segment XI.

Pharyngeal glands penetrate into segment V. Chlorogogen cells begin in segment VI. A pair of diverticulae present on the gut, joining this in the posterior part of segment IX and extending anteriorly to septum VIII/IX. Vasa deferentia, 11 to 14 μ diameter and as long as, or slightly shorter than atria, join latter apically. Atria cylindrical, 110 to 130 μ long, 40 to 55 μ diameter, which narrow to a pair of ducts, 70 to 80 μ long, (relaxed condition), 15 μ diameter. These ducts terminate

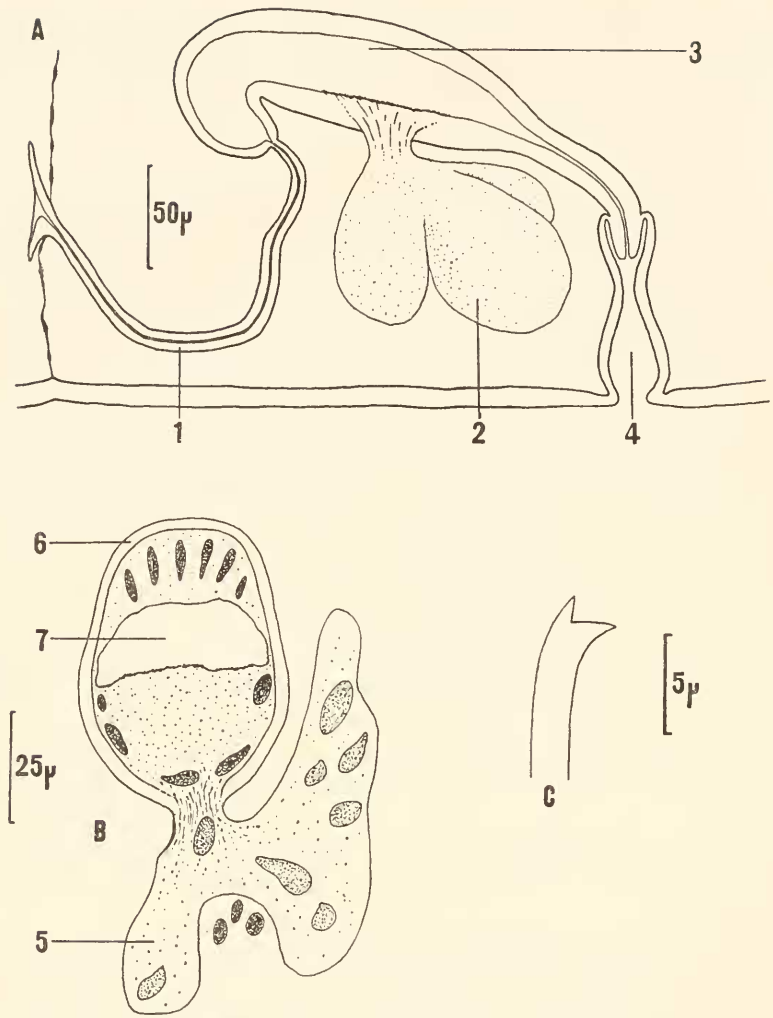

FIGURE 7. *Limnodriloides medioporus* nov. sp. A. Male genitalia; B. Transverse section of atrium and prostate gland; C. Seta. 1. Vas deferens; 2. Prostate; 3. Atrium; 4. Median genital chamber; 5. Prostate cells; 6. Dorsal atrium wall; 7. Atrial lumen.

in small, conical penes, 25 μ long, which open into a median chamber, mediolaterally (Fig. 7a). Long axis of atria directed anteriorly. Large compact prostate glands open into atria medially and ventrally. Lining cells of ventral part of atria thicker than dorsal cells (Fig. 7b). One pair spermathecae with ovoid ampullae and short, ill-defined ducts, present in segment X. Ducts open into common median chamber. Sperm in spermathecae, often oriented in a definite manner and in discrete masses.

DISTRIBUTION. Continental shelf, Massachusetts, USA.

Limnodriloides appendiculatus Pierantoni, 1903

Limnodriloides appendiculatus Pierantoni, 1904, pp. 187–188, fig. 1: Boldt, 1928, pp. 145–151, fig. 2–3: Hrabě, 1967, pp. 339, 344.
Clitellio appendiculatus (Pierantoni). Brinkhurst, 1963a, p. 73; 1963b, p. 713; 1966, p. 300; 1967, p. 115.

Type-material. Not designated and not located. Type-locality; Gulf of Naples, Italy. Depth 3 meters.

Description, (from literature). Length 10 to 18 mm, diameter 0.2 to 0.4 mm. 40 to 50 segments. Clitellum on segments 1/2X to 1/2XII. Setae bifid with upper tooth thinner, and posteriorly shorter, than lower. 2 (rarely 3) setae per bundle anteriorly and 2 posteriorly. No modified genital setae. Male and spermathecal pores situated just anterior to ventral setae of segments X and XI, respectively.

Pharyngeal glands present in segments III to V. Chlorogogen cells begin in segment VI. A pair of intestinal diverticulae present in segment VIII, extending to septum VII/VIII. Vasa deferentia, 13 μ diameter, as long as, or slightly shorter than atria which they join apically. Atria cylindrical, with a median constriction and narrowing proximally. Atria open into a pair of pear-shaped, eversible pseudopenes laterally. Large, discrete, broadly-attached prostate glands join atria subapically. Paired spermathecae in segment X with very short, ill-defined ducts.

Distribution. Known only from type-locality.

Limnodriloides agnes Hrabě, 1966

Limnodriloides agnes Hrabě, 1967, pp. 339–344, fig. 13–24.

Type-material. Syntypes (?) Hrabě collection No. 1766—1, 4. Nesebar (Mesembria), near Fishermans Pier, Black Sea, Bulgaria.

Description, (from literature). Length 10 mm, diameter 0.4 mm. 50 to 68 segments. Prostomium rounded. Clitellum developed on segments 1/2X to XII. Setae bifid with upper tooth shorter and thinner than lower, 2 (rarely 3) per bundle anteriorly, 1 per bundle posteriorly, 77 to 112 μ long. Ventral setae of segment X unmodified, of segment XI absent. Paired spermathecal pores anterior, and a little lateral to ventral setae of segment X. Paired male pores in place of ventral setae of segment XI.

Pharyngeal glands in segments III to IV. Chlorogogen cells begin in segment VI. A pair of intestinal diverticulae present in segment IX which extend to septum VIII/IX. Vasa deferentia shorter than atria which they join apically. Diameter of vasa deferentia near small male funnels, 16 μ widening to 25 μ near atrial junction. Atria elongate and tapering proximally, 38 μ diameter near vasa deferentia, narrowing to 11 μ about half way along its length. Atria open into a pair of large, eversible pseudopenes, 208 μ long, 64 μ diameter. Large, compact, non-pedunculate prostate glands join atria near vasa deferentia. Paired spermathecae with long, cylindrical ampullae and very short, inconspicuous ducts.

Distribution. Known only from type-locality.

Limnodriloides winckelmanni Michaelsen, 1914

Limnodriloides winckelmanni Michaelsen, 1914, pp. 155–160, Pl. V, fig. 6, 7: Boldt, 1928, pp. 146–148, fig. 1: Hrabě, 1967, pp. 339, 345–347, fig. 25–29.
Clitellio winckelmanni (Michaelsen). Brinkhurst, 1963a, p. 73; 1963b, p. 713; 1966, p. 153.

Type-material. Not designated and not yet located. Type-locality, Swakopmund, South West Africa. Intertidal, under stones.

Description, (from literature). Length 12 to 18 mm, diameter 0.2 to 0.25 mm posteriorly and 0.6 mm in clitellar region. 3 setae per bundle anteriorly, 2 per bundle posteriorly, smaller than middle setae. Middle setae 90 μ long, 5 μ thick with lower tooth 5 μ long. 1 ventral modified seta per bundle of segment X; this spermathecal seta hollow, contained in large vacuolated gland cells and surrounded by thick muscle layer. Male and spermathecal pores paired in line of ventral setae.

Paired intestinal diverticulae present in segment IX. Vasa deferentia as long as atria, join latter apically. Atria ovoid with long, narrow, proximal ducts, terminating in small penes (Hrabě, 1967, states that it has no penes but illustrates a penis-like structure). Large prostate gland joins each atrium ventrally on a broad base. Spermathecal ampullae sacciform, with thick, discrete ducts. Sperm oriented into long, narrow bundles.

Distribution. Known only from type-locality.

Spiridion Knollner, 1935

Definition. Hair setae absent. Ventral setae of segment XI modified into a row of penial setae. Male and spermathecal pores paired, more or less in line of ventral setae.

Vasa deferentia about as long as atria. One discrete, pedunculate prostate gland joins each atrium almost apically but dorsal or posterior to junction of vas deferens. Atrial muscle thin. True penes absent. Spermatophores not developed. Coelomocytes absent.

Remarks. No key to species is provided as three out of the four species here attributed to *Spiridion* are *species dubiae*.

Type species: *Spiridion insigne* Knollner, 1935.

Spiridion insigne Knollner, 1935

Spiridion insigne Knollner, 1935, pp. 427, 471–475, fig. 35–38: Bulow, 1957, p. 98: Hrabě, 1960, p. 255, fig. 13–14: Cekanovskaya, 1962, p. 243: Brinkhurst, 1963a, pp. 74, 75, fig. 2, 57; 1967, p. 115.
Spiridon insigne Knollner. Brinkhurst, 1963b, pp. 712, 714.
(?) *Spiridion insigne* Knollner. Brinkhurst, 1965b, p. 153.

TYPE-MATERIAL. Not designated and not located. Type-locality, Strander Bach, Schilkseebucht, Kiel Bay, Baltic Sea, West Germany.

DESCRIPTION, (from literature). Length 5 to 10 mm, diameter 0.34 mm at segment XI, 0.13 mm diameter in pre-clitellar segments. 34 segments. Setae bifid with upper tooth shorter and thinner than lower, 35 to 45 μ long. 3 to 5 setae per bundle anteriorly, 1 to 2 (sometimes 3) posteriorly. 4 to 6 single-pointed, hooked penial setae, 77 to 90 μ long. Ventral setae of segment X absent. Male pores anterior to and in line with penial setae. Spermathecal pores, in line with ventral setae, present in anterior part of segment X.

Vasa deferentia a little longer than atria, join latter apically. Atria cylindrical, 140 μ long, 20 μ diameter. Prostate gland enters atrium near vas deferens. Spermathecae with long, cylindrical ampullae and short discrete ducts which open near septum IX/X.

DISTRIBUTION. Marine littoral Baltic Sea. Ground-water, Germany. West Atlantic coast (?)

Species dubiae

Spiridion scrobicularae Lastockin, 1937

Spiridion scrobicularae Lastockin, 1937, p. 234.

Spiridion scrobiculare Lastockin. Brinkhurst, 1963a, p. 75; 1967, p. 115.

TYPE-MATERIAL. Not designated and not located. Type-locality, Coparskaya Bay, Gulf of Finland, USSR.

DESCRIPTION. Clitellum rudimentary, developed only in region of spermathecal pores and genital cavity. Male pore unpaired, median. Penial setae present. Paired atria muscular, consisting of a narrow anterior part and pear-shaped posterior part. Prostate gland joins atrium apically. Both atria and bundles of penial setae open into the median genital chamber.

DISTRIBUTION. Type-locality only.

Spiridion roseus (Pierantoni, 1903) nov. comb.

Limnodriloides roseus Pierantoni, 1904, pp. 188, 189, fig. 2: Boldt, 1928, pp. 146–148: Hrabě, 1967, p. 347.
Clitellio roseus (Pierantoni). Brinkhurst, 1963a, p. 73; 1963b, p. 713.

TYPE-MATERIAL. Not designated and not located. Type-locality, Gulf of Naples, Italy. Depth 3 to 4 meters.

DESCRIPTION. Setae bifid, 4 per bundle anteriorly, 3 per bundle posteriorly. Vasa deferentia short, join atria apically. Atria elongate, pear-shaped to cylindrical,

erect, terminating in short protrusible penes. Large prostate gland joins each atrium just posterior to junction of vas deferens.

Distribution. Type-locality only.

Spiridion pectinatus (Pierantoni, 1903) nov. comb.

Limnodriloides pectinatus Pierantoni, 1904, pp. 190, 191, fig. 3: Boldt, 1928, pp. 146–148: Hrabě, 1967, p. 347.
Clitellio pectinatus (Pierantoni). Brinkhurst, 1963a, p. 73; 1963b, p. 713.

Type-material. Not designated and not located. Type-locality, Gulf of Naples, Italy.

Description. Length 12 to 15 mm, diameter 0.25 mm. 50 segments. Clitellum on segments 1/2X to 1/2XII. Setae bifid, 4 per bundle up to about segment XIV, then 2 to 3 per bundle. Ventral setae of segment XI modified to 12 small penial setae situated on tubercles. Paired male pores lateral to penial setae. Spermathecal pores in line with and anterior to ventral setae. Short vasa deferentia and large prostate glands join atria apically.
Distribution. Type-locality only.

Discussion

In the generic definition of *Phallodrilus,* coelomocytes were said to be "sparse to absent." *P. coeloprostatus,* for example, possesses a few small, free, darkly-staining cells in the coelom. In *Adelodrilus* the situation is similar. Hrabě (1963; 1966; 1967) has used the presence or absence of coelomocytes as the major character separating his subfamilies Tubificinae and Rhyacodrilinae. Clearly the intermediate condition of *Phallodrilus* and *Adelodrilus* invalidates the erection of subfamilies of Tubificidae on the basis of the presence or absence of coelomocytes.

My gratitude goes to Dr. R. O. Brinkhurst (University of Toronto) and Dr. R. P. Higgins (Systematics-Ecology Program, Marine Biological Laboratory) who offered useful criticism of this manuscript and to Dr. D. C. Grant (Systematics-Ecology Program) who made the Cape Cod Bay material available to me. My gratitude also to Dr. M. R. Carriker with whose program this project was carried out. The investigation was supported by grants from the Ford Foundation and from the National Science Foundation (GB-7387) to the Systematics-Ecology Program, Marine Biological Laboratory.

Summary

1. Marine Tubificidae from Cape Cod Bay, received from the Systematics-Ecology Program's Biotic Census, were examined.

2. One new genus and five new species are described, *Adelodrilus anisosetosus* nov. gen., nov. sp., *Peloscolex intermedius, Limnodriloides medioporus, Phallodrilus obscurus* and *Phallodrilus coeloprostatus.*

3. The genera *Limnodriloides, Phallodrilus* and *Spiridion* are reviewed.

4. *Aktedrilus* is made a junior synonym of *Phallodrilus.*

5. *L. roseus* Pierantoni, 1903 and *L. pectinatus* Pierantoni, 1903 are treated as *species dubiae* of *Spiridion.*

LITERATURE CITED

Boldt, W., 1928. Mitteilung über Oligochaeten der Familie Tubificiden. *Zool. Anz.,* **75**: 145–151.

Brinkhurst, R. O., 1963a. Taxonomical studies on the Tubificidae (Annelida, Oligochaeta). *Int. Rev. Hydrobiol.,* 1963, Syst. Beihefte 2: 1–89.

Brinkhurst, R. O., 1963b. Notes on the brackish-water and marine species of Tubificidae (Annelida, Oligochaeta). *J. Mar. Biol. Ass. U. K.,* **43**: 709–715.

Brinkhurst, R. O., 1963c. A genus of brackish water Oligochaeta new to Britain. *Nature,* **199**: 1206.

Brinkhurst, R. O., 1964. Observations on the biology of the marine Oligochaete *Tubifex costatus* (Clap.). *J. Mar. Biol. Ass. U. K.,* **44**: 11–16.

Brinkhurst, R. O., 1965a. A taxonomic revision of the Phreodrilidae (Oligochaeta). *J. Zool.,* **147**: 363–386.

Brinkhurst, R. O., 1965b. Studies on the North American aquatic Oligochaeta II: Tubificidae. *Proc. Acad. Natur. Sci. Philadelphia,* **117**: 117–172.

Brinkhurst, R. O., 1966. A contribution to the systematics of the marine Tubificidae (Annelida, Oligochaeta). *Biol. Bull.,* **130**: 297–303.

Brinkhurst, R. O., 1967. The Oligochaeta, *in* Limnofauna Europea, 110–117. Berlin.

Bulow, T., 1955. Oligochaeten aus den Endgebieten der Schlei. *Kieler Meerforsch.,* **11**: 253–264.

Bulow, T., 1957. Systematisch-autokologische Studien an eulitoralen Oligochaeten der Kimbrischen Halbinsel. *Kieler Meerforsch.,* **13**: 69–116.

Cain, A. J., 1954. Animal Species and Their Evolution. Hutchinson, London.

Chekanovskaya, O. V., 1962. Aquatic Oligochaetous worms of the fauna of the USSR. *Opredeliteli Faune Zool. Inst. Acad. Nauk. SSSR.,* **78**: 3–411.

Cook, D. G., 1967. Studies on the Lumbriculidae (Oligochaeta) in Britain. *J. Zool.,* **153**: 353–368.

Cook, D. G., 1968. The genera of the family Lumbriculidae Vejdovsky, 1884 and the genus *Dorydrilus* Piguet, 1913 (Annelida, Oligochaeta). *J. Zool.,* (in press).

Hrabě, S., 1960. Oligochaeta limicola from the collection of Dr. S. Husmann. *Spisy Přírodoved Fak. Univ. Brne,* **415**: 245–277.

Hrabě, S., 1963. On *Rhyacodrilus lindbergi* n. sp., a new cavernicolous species of the fam. Tubificidae (Oligochaeta) from Portugal. *Bol. Soc. Port. Cienc. Natur.,* **10**: 52–56.

Hrabě, S., 1966. New or insufficiently known species of the family Tubificidae. *Spisy Přírodoved Fak. Univ. Brne,* **470**: 57–77.

Hrabě, S., 1967. Two new species of the family Tubificidae from the Black Sea, with remarks about various species of the subfamily Tubificinae. *Spisy Přírodoved Fak. Univ. Brne,* **485**: 331–356.

Knollner, F. H., 1935. Okologische und systematische Untersuchungen über litorale und marine Oligochäten der Kieler Bucht. *Zool. Jahrb., (Syst.),* **66**: 425–512.

Lastockin, D., 1937. New species of Oligochaeta limicola in the European part of the USSR. *Dokl. Akad. Nauk. SSSR,* **17**: 233–235.

Michaelsen, W., 1914. Beiträge zur Kenntnis der Land- und Susswasserfauna Deutsch-Sudwestafrikas: Oligochaeta. Hamburg, pp. 139–182.

Moore, J. P., 1905. Some marine Oligochaeta of New England. *Proc. Acad. Natur. Sci. Philadelphia,* **57**: 373–399.

Pierantoni, U., 1903. Due nuovi generi di Oligocheti marini rinvenuti nel Golfo di Napoli. *Boll. Soc. Natur. Napoli,* **16**: 113–117.

Pierantoni, U., 1904. Altri nuovi oligocheti del Golfo di Napoli (*Limnodriloides* n. gen.)—II nota sui Tubificidae. *Boll. Soc. Natur. Napoli,* **17**: 185–192.